Leaf morphology and photosynthetic adjustments among deciduous broad-leaved trees within the vertical canopy profile

TAKAYOSHI KOIKE,[1,2,5] MITSUTOSHI KITAO,[2] YUTAKA MARUYAMA,[2] SHIGETA MORI[2,3] and THOMAS T. LEI[2,4]

[1] *Hokkaido University Forests, Sapporo 060-0809, Japan*

[2] *Forestry and Forest Products Research Institute (FFPRI), Sapporo 062-8516, Japan*

[3] *FFPRI, Morioka 020-0123, Japan*

[4] *Present address: CSIRO Cotton Research Unit, Locked Bag 59, Narrabri, NSW 2390, Australia*

[5] *Author to whom correspondance should be addressed*

Summary Photosynthetic acclimation of deciduous broad-leaved tree species was studied along a vertical gradient within the canopy of a multi-species deciduous forest in northern Japan. We investigated variations in (1) local light regime and CO_2 concentration ($[CO_2]$), and (2) morphological (area, thickness and area per mass), biochemical (nitrogen and chlorophyll concentrations) and physiological (light-saturated photosynthetic rate) attributes of leaves of seven major species on three occasions (June, August and October). We studied early successional species, alder (*Alnus hirsuta* (Spach) Rupr.) and birch (*Betula platyphylla* var. *japonica* (Miq.) Hara); gap phase species, walnut (*Juglans ailanthifolia* Carrière) and ash (*Fraxinus mandshurica* var. *japonica* Rupr.); mid-successional species, basswood (*Tilia japonica* (Miq.) Simonk.) and elm (*Ulmus davidiana* var. *japonica* (Rehd.) Nakai); and the late-successional species, maple (*Acer mono* Bunge). All but maple initiated leaf unfolding from the lower part of the crown. The $[CO_2]$ within the vertical profile ranged from 320–350 ppm in the upper canopy to 405–560 ppm near the ground. The lowest and highest ambient $[CO_2]$ occured during the day and during the night, respectively. This trend was observed consistently during the summer, but not when trees were leafless. Chlorophyll concentration was positively related to maximum photosynthetic rate within, but not among, species. Leaf senescence started from the inner part of the crown in alder and birch, but started either in the outer or top portion of the canopy of ash, basswood and maple. Chlorophyll (Chl) to nitrogen ratio in leaves increased with decreasing photon flux density. However, Chl b concentration in all species remained stable until the beginning of leaf senescence. Maximum photosynthetic rates observed in sun leaves of early successional species, gap phase or mid-successional species, and late successional species were 12.5–14.8 μmol m^{-2} s^{-1}, 4.1–7.8 μmol m^{-2} s^{-1} and 3.1 μmol m^{-2} s^{-1}, respectively.

Introduction

A forest has its own vertical micro-environmental gradients (Elias et al 1989, Ellsworth and Reich 1993, Parker 1995). Diurnal and seasonal changes in the physical environment within the canopy affect the physiological activities of both trees and soil microorganisms. In cool temperate regions, temperature, carbon dioxide concentration ($[CO_2]$) and photon flux density in deciduous broad-leaved forests are greatly modified by the seasonality of leaf development (Marek et al. 1989, Holbrook and Lund 1995). Given the mixture of canopy species with substantially different gas exchange capacities (Koike 1988, Niinemets 1997), an assessment of the species-specific photosynthetic capacity of individual leaves may facilitate the scaling up of biomass production to the stand level. In the past, determination of the maximum photosynthetic rate of the exposed crown was considered sufficient (Saeki 1960) to estimate the CO_2 flux of a forest. However, in recent investigations, different light and water utilization capacities among species within the canopy gradient have been reported (Bassow and Bazzaz 1997, Hanba et al. 1997). Moreover, a positive relationship between photosynthetic capacity and leaf nitrogen content (Evans 1989, Hikosaka and Terashima 1998) means that the "big leaf" (Kull and Kruijt 1999) idea of canopy properties may be oversimplified. Heterogeneity of a forest stand usually results in complexity in the dynamics of CO_2 fixation (Bassow and Bazzaz 1998). Therefore, an improved assessment of whole-canopy biomass production may require elucidation of species-specific differences in leaf morphology, biochemistry and whole-tree physiology within the forest canopy profile.

Estimates of biomass production and CO_2 flux in a mono-

specific even-aged forest have been achieved by modeling the interaction between the micro-environment and canopy photosynthetic activities (Waring et al. 1995). Such estimates (i.e., photosynthetic capacity and biomass production) for temperate forests can assist in defining their role in global carbon cycles (Houghton 1991, Wofsy et al. 1993, Bassow and Bazzaz 1997, 1998). However, canopy photosynthesis is a function of leaf nitrogen and chlorophyll distribution within the canopy profile. In general, shade leaves allocate more nitrogen to chlorophyll, thereby increasing the efficiency of incident light capture (Osmond et al. 1980, Boardman 1981, Kimura et al. 1998). We would expect, therefore, a stratified acclimation within the canopy profile that differs among species according to their individual patterns of canopy development. For example, the leaf senescence pattern of a tree crown is closely linked to the growth strategy of the species. There is a clear contrast in the progression of autumn coloration between early successional species, which starts from the inner part of the crown, and late successional species, which starts from the outer surface of the crown (Koike 1990). Variation in pattern of late-season nitrogen translocation among senescence types may affect shade acclimation and seasonal biomass production.

The outer crowns of canopy trees experience high irradiances, vapor pressure deficits, temperature fluctuations, and periodically low [CO_2] (Parker 1995). With increasing proximity to the canopy top, leaf water stress may limit photosynthetic activity (Horton and Hart 1998), leading to midday depression of gas exchange (Wofsy et al. 1993, Holbrook and Lund 1995, Bassow and Bazzaz 1998, Hiromi et al. 1999). Excessive accumulation of carbohydrate may also lower canopy photosynthetic rate.

This study examined the capacity of forest tree foliage to acclimate morphologically and photosynthetically in relation to the vertical foliage profile of overstory trees in a secondary forest. Particular objectives were to: (1) monitor the seasonal trend in micro-climatic factors associated with canopy leaf development; (2) assess photosynthetic leaf acclimation along the vertical canopy profile by measuring SLA, leaf N and Chl concentrations, and light-saturated photosynthetic rates for leaves of seven tree species; and (3) measure the photosynthesis–light response curves of leaves located in the sunny and shady crown areas.

Materials and methods

Site and species

The study site was located in the experimental forest of the Forestry and Forest Products Research Institute in Sapporo, Japan (42°58′ N, 141°23′ E, 160 m a.s.l., Koike et al. 1998). Mean annual precipitation is 1200 mm. Maximum recorded snow depth is 2.6 m. Mean annual temperature is 6.1 °C (max. 28 °C; min. –16 °C). Ash (*Fraxinus mandshurica* var. *japonica* Rupr.), elm (*Ulmus davidiana* var. *japonica* (Rehd.) Nakai) and alder (*Alnus hirsuta* (Spach) Rupr.) were the dominant tree species in this north-temperate forest (Hanba et al.

1997, Koike et al.1998). Mean tree height was 18.5 m and mean stem diameter at breast height was 15.8 cm (SD 11.2).

We constructed a 24-m-high monitoring tower (with a 5 × 5-m base) where seven canopy tree species could be accessed. The species were walnut (*Juglans ailanthifolia* Carrière), alder, white birch (*Betula platyphylla* var. *japonica* (Miq.) Hara), basswood (*Tilia japonica* (Miq.) Simonk.), maple (*Acer mono* Bunge), elm and ash. Other species near the tower included oak (*Quercus mongolica* var. *grosseserrata* Fisch. *ex* Turcz), dogwood (*Cornus contraversa* Hemsl.) and kalopanax (*Kalopanax pictus* (Thunb.) Nakai.). Until 1996, trees selected for measurement were limited to those around the single monitoring tower. Given the limitation in the number of sampled trees, we acknowledge that the design suffers from pseudo-replication (Hurlbert 1984, Terazawa and Kikuzawa 1994). In 1996, we measured the maximum photosynthetic rates and photosynthetic light response curves of canopy trees, using leaves on upper canopy branches that were pulled within reach of the monitoring tower by means of ropes. In 2000, the upper canopy was accessed by climbing the trees.

The sampled species vary in their successional traits (Kikuzawa 1983, Koike 1988). The successional types, with the species and number of individuals sampled in parenthesis, were early successional species, alder (3) and white birch (3); mid-successional or gap phase species, ash (4), elm (3) and walnut (2); and late successional species, maple (4) and basswood (3). Naturally regenerated saplings (height of about 1.5 m) of five ash, four maples and four walnuts were also measured. We compared the specific responses of leaves to various environmental factors, assuming that interspecific variation is larger than intraspecific variation (Bassow and Bazzaz 1997).

Vertical profiles of light and carbon dioxide concentration

Photosynthetic photon flux density (PPFD) and [CO_2] were monitored at heights of 0.5, 2, 4, 10, 14, 18 and 24 m. Irradiance was recorded continuously with quantum sensors ("solar monitor," Kyokko Trade Co., Tokyo, Japan). Relative PFD (RPFD), i.e, relative to that above the canopy, was calculated from the integrated value for approximately 1 month (i.e., data for June were from May 2 to June 12, August data were from July 1 to August 2, and October data were from September 2 to October 4 in 1996). Carbon dioxide concentrations were measured with an infrared gas analyzer (ZDF, Fuji Elect. Co., Tokyo, Japan) with a 6-channel auto-sampler (DAIWA Air Regulation Co. Ltd., Sapporo, Japan). Carbon dioxide concentration at each height was monitored for 1 min every 21 min.

Photosynthetic measurement

The photosynthetic light response curve was measured with an open system portable infrared gas analyzer (IRGA, ADC H3, Hoddesdon, Herts., U.K.). A closed system portable IRGA (Li-Cor Inc., LI-6200, Lincoln, NE) was used to determine the maximum photosynthetic rates of individual attached leaves (at saturated PPFD of 600 µmol m^{-2} s^{-1} for late successional species and 1000 µmol m^{-2} s^{-1} for early successional species; ambient [CO_2] was about 350 ppm and VPD was about

1.4 kPa). Photosynthetic measurements were started from the canopy top at around 0830 to 0900 h, which was about 2.5 h after sunrise. Sampling of the lower canopy occurred at about 1300 h. When we measured the light-dependent photosynthetic rate, saturated light was provided either by direct sunlight at the top of the canopy or by incandescent lamps in the lower canopy. The photosynthetic light response curves of sun and shade leaves during August were made by placing shade cloth (Kuraray shading cloths, Osaka, Japan) above the leaf chamber. The mean ambient temperature for all measurements was 27 °C.

SLA and leaf Chl and N concentrations

Leaf area was determined with an area meter (LI-300) following photosynthesis measurements. Measured leaves were dried at 85 °C for 24 h for subsequent dry mass and chemical analysis. Leaf chlorophyll content was determined in dimethyl sulfoxide (DMSO) extracts (Barnes et al. 1992, Shinano et al. 1996). Chlorophylls a and b, and total chlorophyll (Chl a + b) were calculated from absorbance (A) readings at two wavelengths (subscript, in nm):

$$Chl\ a = 14.85 \times A_{664.9} - 5.14 \times A_{648.2}, \tag{1}$$

$$Chl\ b = 25.48 \times A_{648.2} - 7.36 \times A_{664.9}, \tag{2}$$

$$Chl\ a + b = 7.49 \times A_{664.9} + 20.3 \times A_{648.2}. \tag{3}$$

Leaf N concentration and C/N ratio were determined with a C/N autoanalyzer (C/N corder, Sumica NT-800, Sumitomo Chemical, Osaka, Japan) and gas chromatograph (Shimadzu GLG 800, Kyoto, Japan).

Seasonal trends in net photosynthetic rate and leaf chlorophyll and N concentrations were measured between June 15–18, August 3–6 and October 2–4 in 1996. Analysis of the relationship between leaf morphology, chlorophyll concentration and net photosynthetic rate was carried out during the period August 4–6.

Results

Physical environment associated with leaf phenology

Seasonal change in the RPFD coincided with leaf phenology and the developmental dynamics of tree leaves (Figure 1A). Irradiance increased to about 20 MJ m^{-2} day^{-1} in mid-April, peaked at about 23 MJ m^{-2} day^{-1} in June and decreased to 5 MJ m^{-2} day^{-1} in late October. Canopy trees, such as alder, birch and elm, started leaf unfolding in early May (Figure 2). After leaf unfolding, RPFD decreased from 72 to 49% at 18 m (canopy top), and from 32 to 13% at 10 m (middle canopy of sub-canopy trees). Among the seven species studied, all but maple initiated leaf unfolding from the lower part of the crown. In birch, late leaves developed about 2 weeks after the flush of early leaves. Ash leaves flushed 2 weeks later, in early June, and leaves continued to emerge until early July. Alder started leaf shedding in mid-July when leaves were still green.

In other species, except ash, leaf senescence (yellowing of leaves) began in late September and all leaves, except for those of alder and birch, were shed by late October or early November. Senescence in ash occurred earlier and more rapidly and all leaves were shed by early September. Alder retained some green leaves at the top of the canopy until early November. Leaf expansion in saplings occurred at almost the same time as in canopy trees. However, leaf shedding started 1 to 2 weeks later in saplings than in canopy trees. After leaf yellowing in most canopy trees and completion of leaf shedding in ash, RPFD increased from 49 to 85% at 18 m, and from 13 to 21% at 10 m.

During the summer, [CO$_2$] varied greatly across the vertical canopy profile and diurnally, especially near the ground (Figure 1B). The [CO$_2$] within the vertical profile ranged from 320–350 ppm in the upper canopy (at 14–16 m) to 405–560 ppm near the ground (at 0.5–4 m). The lowest and highest values of ambient [CO$_2$] were observed during the day and during the night, respectively. The largest variation in [CO$_2$] was found in the lower canopy (0.5–4 m). When trees were leafless, there was no consistent variation in [CO$_2$] with height.

Leaf characteristics within the vertical canopy profile

Individual leaf area generally increased from canopy top to ground level (Figure 3A). The trend was strongest in basswood and elm, and weakest in walnut and birch. Except for walnut, leaf thickness decreased with RPFD down the canopy profile. The light-dependent change in leaf thickness was largest in elm and ash and smallest in walnut (Figure 3B). In conjunction with changes in leaf thickness, there was an increase in specific leaf area (SLA) with decreasing RPFD (Figure 3C). Before autumn coloration took place, SLA increased in all species except alder.

Leaf chlorophyll concentration (Chl) of ash, birch and elm was highest in the mid-canopy (15 m) and in the shady portion of the upper canopy (Figure 4). Chlorophyll concentration of alder and walnut was highest in the topmost canopy leaves. By October, upper canopy leaves of ash and walnut had been shed. In other species, there was an overall decrease in leaf Chl concentration within the canopy profile, and the pattern of Chl distribution was unchanged throughout the season. Alder maintained a markedly high leaf Chl concentration even in the latter part of the growing season.

Chlorophyll b concentration (Chl b) is indicative of acclimation of leaves to shade, because it is usually the main component of the LHCP. Chlorophyll b concentration (Chl b) was maintained at a stable value throughout the growing season in all species except walnut (Figure 5). The vertical variation of leaf Chl b concentration within species was slight. Leaf Chl b concentration of alder and walnut was about 100 mg m^{-2}, but was about 50 mg m^{-2} for other species.

Leaf nitrogen concentration showed a similar trend to total chlorophyll concentration during the growing period (data not shown). An increase in nitrogen allocation to chlorophyll indicates adaptation to shady conditions. The Chl/N ratio calcu-
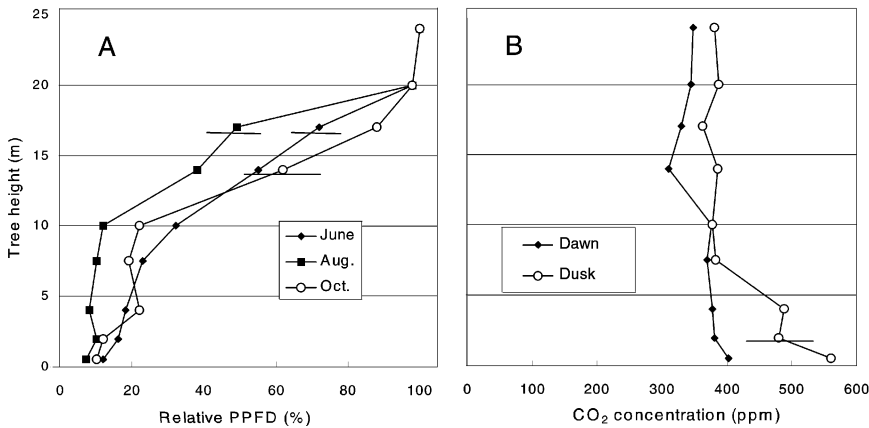
Figure 1. Ambient light (A) and [CO_2] (B) within the forest canopy profile. Dawn and dusk occured at about 1030 and 2030 h, respectively. Bars indicate the maximum standard error.

lated in August showed an increase in Chl/N ratio with decreasing RPFD in all species (Figure 6). The Chl/N ratio measured in June for basswood, elm and maple increased to 0.4 to 0.5, especially in the lower part of the canopy, whereas the Chl/N ratio in alder and birch was around 0.2. In October, the Chl/N ratio of leaves of most species was highly variable, reflecting variation in the time of onset of leaf yellowing. Similar variability was seen in August in maple and elm species. Alder maintained smaller Chl/N values of around 0.16–0.21.

Photosynthetic characteristics

Variation in light-saturated net photosynthetic rate (P_{max}) within the vertical canopy profile for ash, basswood and elm was not significant in June and October. In August, except for walnut, P_{max} at the canopy top was lower than at 3 m below the canopy top (Figure 7). The change in net photosynthetic rate between sun and shade leaves within the crown of walnut was weaker than in the other species. By October, the onset of senescence resulted in a substantial decline in photosynthetic rates in all species compared to mid-season values. For ash, elm and walnut, light-saturated photosynthetic rate at the top of the canopy was lower than in the lower canopy. Within the canopy profile, the range of leaf internal [CO_2] was 245–305 ppm for all tree species measured on sunny, midsummer days.

The difference in light-saturated photosynthetic rate between sun and shade leaves within the crown was greater for early successional species, such as alder and birch (Figure 8). The difference was smaller for the late or mid-successional species of maple and basswood. For early successional species, photosynthesis was light saturated at around 1000–1200 μmol m^{-2} s^{-1} for sun leaves at the top of the canopy and 800–900 μmol m^{-2} s^{-1} for shade leaves lower in the crown.
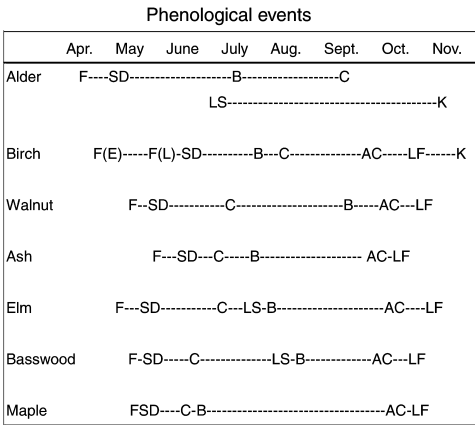

Figure 2. Leaf phenology of canopy trees in a deciduous broad-leaved forest. Abbreviations: F = leaf flush, E = early leaf unfolding, L = late leaf unfolding, SD = shoot development, C = cessation of shoot development, B = bud formation observed, LS = leaf shedding, AC = autumn coloration, LF = leaf fall, K = killed by frost. The broken line signifies a continuing process.
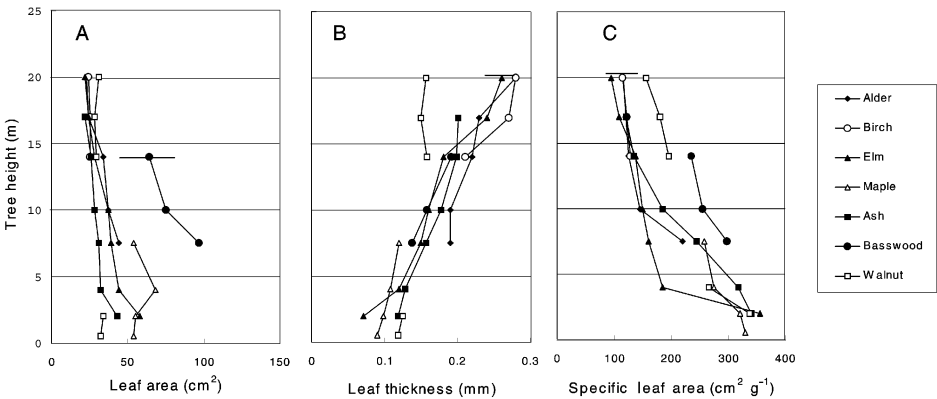

Figure 3. Variation in leaf characteristic of seven tree species within the canopy profiles. (A) Leaf area of all species. (B) Leaf thickness. (C) Specific leaf area (SLA). All measurements were taken in mid-August. Bars indicate the maximum standard error.
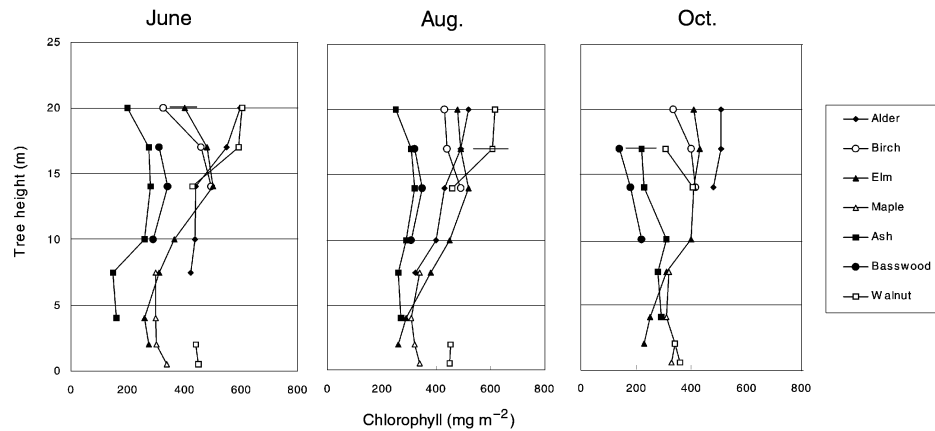
Figure 4. Seasonal changes in the vertical profile of total chlorophyll concentration in leaves of seven deciduous species. Bars indicate the maximum standard error.
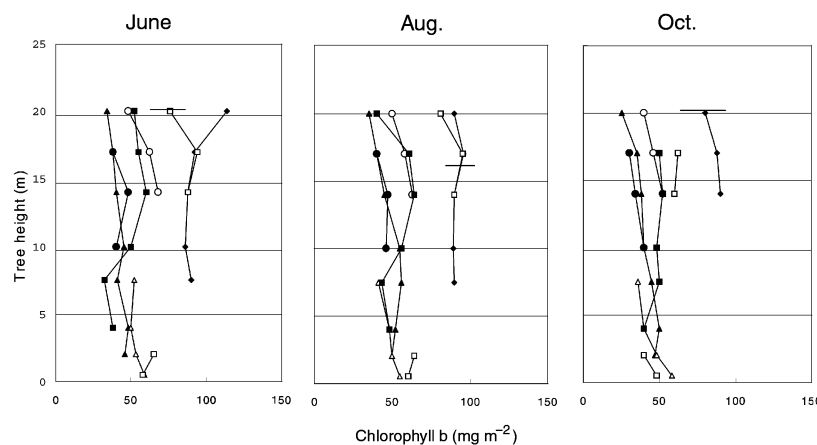

Figure 5. Seasonal changes in chlorophyll b concentration within the canopy profile in seven deciduous tree species. Bars indicate the maximum standard error.

Saturating PPFD was lower in late successional species (400–500 μmol m^{-2} s^{-1}) for both sun and shade leaves. Mid-successional species (elm) or gap phase species (walnut and ash) had light requirements that were intermediate between early and late successional species (basswood and maple). Sun leaves of ash, walnut and basswood showed signs of photo-inhibition, i.e., net photosynthetic rate decreased with increasing PPFD above the saturation value. Slight photoinhibition was seen also in maple.

A positive correlation between P_{max} and leaf nitrogen concentration in August was found (Figure 8). However, the slope of the regression of leaf nitrogen concentration versus P_{max} of elm was of less than in the other species. Sun leaves had higher leaf nitrogen concentration and P_{max} than shade leaves. There was no clear correlation observed between these parameters measured in June and October.
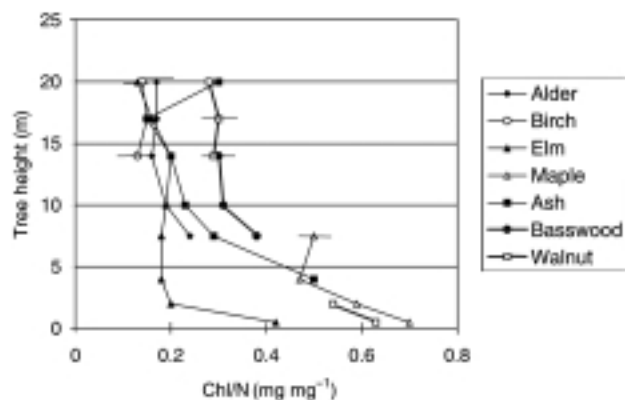
Discussion

Photosynthetic photon flux density within the forest stand is strongly influenced by the leaf developmental pattern of the constituent canopy species. Crown properties such as tree height, species composition, and branch or foliage distribution are highly heterogeneous within the canopy profile. Non-uniformity is the result of species-specific differences in growth pattern and shade tolerance. The divergence among the species within the vertical canopy profile during forest development is termed "differentiation" (Bicknell 1982). Even within a species, there is distinct leaf-level differentiation in physiology and morphology within the canopy profile (Figures 3 and 4). At the species level, the indeterminate leaf production in alder results in a multi-layered crown, whereas the single

Figure 6. Vertical patterns of leaf chlorophyll to nitrogen ratio (Chl/N) of different tree species. Bars indicate the maximum standard error.
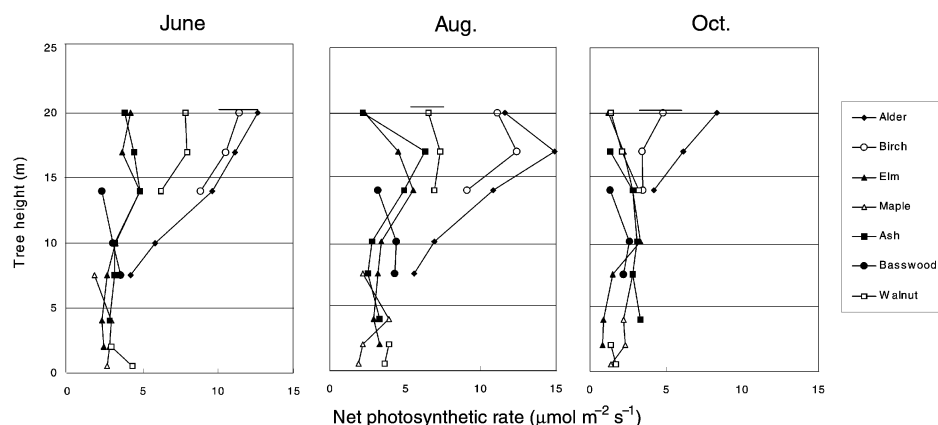
Figure 7. Seasonal and vertical changes in light-saturated photosynthetic rate of seven deciduous species in a forest stand. Bars indicate the maximum standard error.

leaf flush characteristics of maple result in a mono-layered crown (Kikuzawa 1983, Koike 1988, Kuppers 1989). These specific crown shapes can modify light quality and quantity in the forest understory (Lei et al. 1998). Local variation in the light environment can induce further differentiation of leaf distribution within the crown (Reich et al. 1990, Ellsworth and Reich 1993).
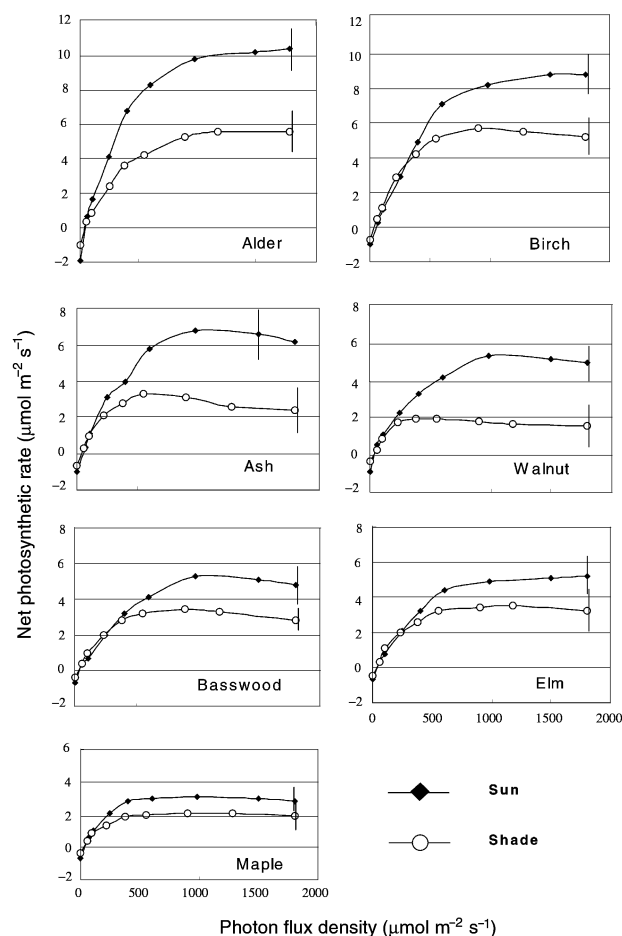

Figure 8. The light-dependent net photosynthetic rate of seven tree species. Bars indicate the maximum standard error.

Numerous reports of photosynthetic light curves are available for tree seedlings (Bazzaz and Carlson 1982, Koike 1986) and saplings. However, there are few reports of photosynthetic light response curves for mature forest trees (Holbrook and Lund 1995, Bassow and Bazzaz 1997, 1998, LeRoux et al. 1999). Based on the limited number of examples, the photosynthetic capacity of a forest stand is a function of the combined effects of the CO_2 and light environment. For seedlings and saplings, the large diurnal variation in $[CO_2]$ and the frequency of sunflecks are particularly critical to their success in becoming canopy trees (Elis et al. 1989, Marek et al. 1989, Holbrook and Lund 1995, Parker 1995). According to Figure 1, high near-ground $[CO_2]$ may be conducive to the survival of regenerated seedlings that use incident light efficiently (Elis et al. 1989).

We found that the light environment is a determinant of water-use efficiency or stomatal regulation in the same forest stand as revealed by stable isotope analysis (^{12}C/^{13}C) of leaves (Hanba et al. 1997). It appears that high water-use efficiency permits greater photosynthetic production with decreasing PPFD.

The acclimation potential of each canopy species is expressed largely as plasticity in leaf characteristics, such as leaf size, leaf thickness and chlorophyll and nitrogen concentrations (Figures 3–5). These characteristics are closely linked to the photosynthetic capacity of each species (Bazzaz and Carlson 1982, Koike 1988). In general, except for the canopy top, leaf nitrogen is distributed in relation to the light gradient, (Hirose and Werger 1987, LeRoux et al. 1999, Schoettle and Smith 1999). The range of plasticity in leaf thickness and leaf area appears to be species-specific (Koike 1986), i.e., narrower for alder and broader for basswood or walnut. With a crown shape intermediate between the multi- and mono-layered types, walnut may have a high capacity for adaptation to the light environment within the canopy profile. Light acclimation was also found in the allocation of leaf nitrogen to chlorophyll as indicated by the Chl/N ratio. With decreasing RPFD, Chl/N of all species increased except for alder. The same trend was reported for a Japanese beech (*Fagus japonica* Maxim.) stand (Kimura et al. 1998). Such physiological adjustments increase the efficiency of incident light capture

(Bjorkman 1981). Leaf internal $[CO_2]$ (C_i) of most leaves in early and late growing season was higher than in August. A uniform value of C_i in August implies temporal variation in homeostatic regulation of leaves to the microenvironment.

The highest P_{max} was found a few meters below the canopy top in August, although adequate chlorophyll and nitrogen were present in the uppermost canopy leaves (Figures 7 and 9). Evidence of photoinhibition has been observed in mono-layered canopy tree species such as maple (Shimizu et al., TOEF, Hokkaido University, Japan; unpublished data). Maintenance of leaf water status of maple and other shade-tolerant species may be insufficient at the top of the canopy to allow maximum photosynthesis (Koike 1988, 1990). In these species, the top leaf layer appears to shade leaves just below sufficiently to provide the optimal irradiance.

During the process of chlorophyll degradation in senescing leaves, Chl b concentration was maintained at a stable value even late in the growing season. Because Chl b acts as an antenna pigment to accumulate light (Elias and Masarovicova 1980, Kura-Hotta et al. 1987, Koike 1990, Lei et al. 1996), a stable Chl b concentration may promote late season carbon gain. However, if carboxylation efficiency is already degraded, maintenance of Chl b concentration may result in excess light energy capture.

In conclusion, we found that vertical differentiation of leaf structure and function among canopy species was well developed. The morphological and physiological differentiation of each species in the mixed broad-leaved forest occurs in accordance with the changing light condition within the canopy. Crown structure, i.e., multi- or mono-layered canopy, appears to provide an efficient use of the light available in different strata of the upper canopy. Canopy surface leaves of mono-layered species may act to shield lower leaves from light that is excessive for shade-tolerant species because of inherent phenotypic limitations, e.g., thin leaves.

References

Auge, R.M., X. Duan, J.L. Croker, W.T. Witte and C.D. Green. 1998. Foliar dehydration tolerance of twelve deciduous tree species. J. Exp. Bot. 49:753–759.

Barnes, J. D., L. Balaguer, E. Manrique, S. Elvira, and A.W. Davison. 1992. A reappraisal of the use of DMSO for the extraction and determination of chlorophylls a and b in lichens and higher plants. Environ. Exp. Bot. 85–100.

Bassow, S.L. and F.A. Bazzaz. 1997. Intra- and inter-specific variation in canopy photosynthesis in a mixed deciduous forest. Oecologia 109:507–515.

Bassow, S.L. and F.A. Bazzaz. 1998. How environmental conditions affect canopy leaf-level photosynthesis in four deciduous tree species. Ecology 79:2660–2675.

Bazzaz, F.A. and R.W. Carlson. 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. Oecologia 54:313–316.

Bazzaz, F.A., S.L. Bassow, G.M. Berntson and S.C. Thomas. 1996. Elevated CO_2 and terrestrial vegetation: implications for and beyond the global carbon budget. *In* Global Change and Terrestrial Ecosystems. Eds. Walker, B. and W. Steffen. Academic Press, San Diego, pp 43–76.

Bicknell, S.H. 1982. Development of canopy stratification during early succession in northern hardwoods. For. Ecol. Manage. 4: 41–51.

Bjorkman, O. 1981. Responses to different quantum flux density. *In* Encyclopedia Plant Physiol. N.S. 12A. Springer-Verlag, Berlin, pp 57–107.

Boardman, N.K. 1981. Comparative photosynthesis of sun and shade plants. Annu. Rev. Plant Physiol. 28:355–377.

Elias, P., I. Kratochvilova, D. Janous, M. Marek and E. Masarovicova. 1989. Stand microclimate and physiological activity of tree leaves in an oak-hornbeam forest. I. Stand microclimate. Trees 4: 227–233.

Elias, P. and E. Masarovicova. 1980. Chlorophyll content in leaves of plants in an oak-hornbeam forest. 3. Trees. Photosynthetica 14: 604–610.

Ellsworth, D.S. and P.B. Reich. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96:169–178.

Evans, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78:9–19.

Hanba, Y.T., S. Mori, T.T. Lei, T. Koike and E. Wada. 1997. Variations in leaf $\delta^{13}C$ along a vertical profile of irradiance in a temperate Japanese forest. Oecologia 110:253–261.

Hikosaka, K., Y.T. Hanba, T. Hirose and I. Terashima. 1998. Photosynthetic nitrogen-use efficiency in leaves of woody and herbaceous species. Funct. Ecol. 12:869–905.

Hinckley, T.M., R.G. Aslin, R.R. Aubuchon, C.L. Metcalf and J.E. Roberts. 1978. Leaf conductance and photosynthesis of four species of the oak–hickory forest type. For. Sci. 24:73–84.

Hiromi, T., I. Ninomiya, T. Koike and K. Ogino. 1999. Stomatal regulation of canopy trees in a tropical rain forest. Jpn. J. Ecol. 49: 68–76.
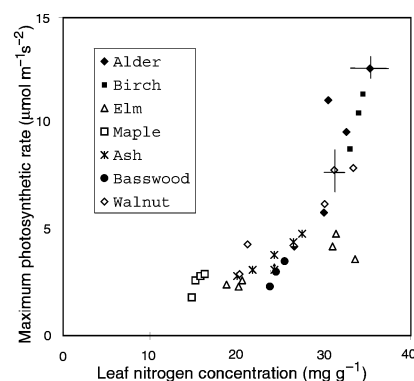
Figure 9. A positive correlation between maximum photosynthetic rate (P_{max}) and leaf nitrogen concentration in August. Bars indicate the maximum standard error.

Hirose, T. and M.J.A. Werger. 1987. Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. Oecologia 72:520–526.

Horton, J.L. and S.C. Hart. 1998. Hydraulic lift: a potentially important ecosystem process. Trends Ecol. Evol. 13:232–235.

Holbrook, N.M. and C.P. Lund. 1995. Photosynthesis in forest canopies. *In* Forest Canopies. Eds. D. Margaret, M.D. Lowman and N.M. Nadkarni. Academic Press, San Diego, pp 411–430.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187–211.

Jurik, T.W. 1986. Seasonal patterns of leaf photosynthetic capacity in successional northern hardwood tree species. Am. J. Bot. 73: 131–138.

Jurik, T.W., J.A. Weber and D.M. Gates. 1988. Effects of temperature and light on photosynthesis of dominant species of a northern hardwood forest. Bot. Gaz. 149:203–208.

Kikuzawa, K. 1983. Leaf survival of woody plants in deciduous broad-leaved forests. 1. Tall trees. Can. J. Bot. 61:2133–2139.

Kimura, K., A. Ishida, A. Uemura, Y. Matsumoto and I. Terashima. 1998. Effects of current-year and previous-year PPFDs on shoot gross morphology and leaf properties in *Fagis japonica*. Tree Physiol. 18:459–466.

Kitajima, K., S.S. Mulkey and S.J. Write. 1997. Seasonal leaf phenotypes in the canopy of a tropical dry forest: photosynthetic characteristics and associated traits. Oecologia 109:490–498.

Kitao, M., T.T. Lei, T. Koike, H. Tobita and Y. Maruyama. 2000. Susceptibility to photoinhibition of three deciduous broadleaf tree species with different successional traits raised under various light regimes. Plant Cell Environ. 23:81–89.

Kitaoka, S., S. Okuyama, A. Naniwa and T. Koike. 2000. Seasonal photosynthetic nitrogen use efficiency of seedlings regenerated under deciduous broadleaved forests in northern Japan. Trans. Jpn. For. Soc., 111:276.

Koike, T. 1986. Photosynthetic responses to light intensity of deciduous broad-leaved tree seedlings raised under various artificial shade. Environ. Cont. Biol. 24:51–58.

Koike, T. 1988. Leaf structure and photosynthetic performance as related to the forest succession of deciduous broad-leaved trees. Plant Species Biol. 3:77–87.

Koike, T. 1990. Autumn coloring, photosynthetic performance and leaf development of deciduous broad-leaved trees in relation to forest succession. Tree Physiol. 7:21–32.

Koike, T., R. Tabuchi, S. Mori, K. Takahashi and T.T. Lei. 1998. Characteristics of the light response in seedlings and saplings of two mid-successional species, ash and kalopanax, during the early stage of regeneration in a mature forest. J. Sustain. For. 6: 73–84.

Kull, O. and Ü. Niinemets. 1998. Distribution of leaf photosynthetic properties in tree canopies: comparison of species with different shade tolerance. Funct. Ecol. 12:472–479.

Kull, O. and B. Kruijt. 1999. Acclimation of photosynthesis to light: a mechanistic approach. Funct. Ecol. 13:24–36.

Kuppers, M. 1989. Ecological significance of above-ground architectural patterns in woody plants: a question of cost-benefit relationships. Trends Ecol. Evol. 4:375–379.

Kura-Hotta, R., M. Okada and S. Kato. 1987. Chlorophyll concentration and its changes in leaves of spinach raised under different light levels. Plant Cell Physiol. 87:12–19.

Lei, T.T., M. Kitao, R. Tabuchi and T. Koike. 1996. Functional relationship between chlorophyll content and leaf reflectance, and light-capturing efficiency of Japanese forest species. Physiol. Plant. 96:411–448.

Lei, T.T., R. Tabuchi, M. Kitao, K. Takahashi and T. Koike. 1998. Effects of weather, season and vertical position on the variation in light quality and quantity in a Japanese deciduous broadleaf forest. J. Sustain. For. 6:35–55.

LeRoux, X., H. Sinoquet and M.Vandame. 1999. Spatial distribution of leaf dry weight per area and leaf nitrogen concentration in relation to local radiation regime within an isolated tree crown. Tree Physiol. 19:181–188.

Long, S.P., S. Humphries and P.G. Falkowski. 1994. Photoinhibition of photosynthesis in nature. Annu. Rev. Plant Physiol. Plant Mol. Biol. 45:633–662.

Marek, M., E. Masarovicova, I. Kratochvilova, P. Elias and D. Janous. 1989. Stand microclimate and physiological activity of tree leaves in an oak–hornbeam forest. II. Leaf photosynthetic activity. Trees 4:227–233.

Niinemets, Ü. 1997. Role of foliar nitrogen in light harvesting and shade tolerance of four temperature deciduous woody species. Funct. Ecol. 11:518–531.

Niinemets, Ü., W. Bilger, O. Kull and J.D. Tenhunen. 1998*a*. Acclimation to high irradiance in temperate deciduous trees in the field: change in xanthophyll cycle pool size and in photosynthetic capacity along a canopy light gradient. Plant Cell Environ. 21: 1205–1218.

Niinemets, Ü., O. Kull and J.D. Tenhunen. 1998*b*. An analysis of light effects on foliar morphology, physiology, and light interception in temperate deciduous woody species of contrasting shade tolerance. Tree Physiol. 18:681–696.

Osmond, C.B., O. Bjorkman and D.J. Anderson. 1980. Physiological processes in plant ecology. Toward a Synthesis with *Atriplex*. Springer-Verlag, Berlin, Heidelberg, pp 468.

Parker, G.G. 1995. Structure and microclimate of forest canopies. *In* Forest Canopies. Eds. D. Margaret, M.D. Lowman and N.M. Nadkarni. Academic Press, San Diego, pp. 73–106.

Reich, P.B., D.S. Ellsworth, B.D. Kloeppel, J.H. Fownes and S.T. Gower. 1990. Vertical variation in canopy structure and CO_2 exchange of oak-maple forest: influence of ozone, nitrogen, and other factors on simulated canopy carbon gain. Tree Physiol. 7: 329–345.

Saeki, T. 1960. Leaf growth as influenced by dry matter production. Bot. Mag. Tokyo 74:70–78.

Schoettle, A.W. and W.K. Smith. 1999. Interrelationships among light, photosynthesis and nitrogen in the crown of mature *Pinus contorta* ssp. *latifolia*. Tree Physiol. 19:13–22.

Shinano, T., T.T. Lei, T. Kawanukai, M.T. Inoue, T. Koike and T. Tadano. 1996. Dimethylsulfoxide method for the extraction of chlorophylls a and b from the leaves of wheat, field bean, dwarf bamboo, and oak. Photosynthetica 32:409–415.

Terazawa, K. and K. Kikuzawa. 1994. Effects of flooding on leaf dynamics and other seedling responses in flood-tolerant *Alnus japonica* and flood-intolerant *Betula platyphylla* var. *japonica*. Tree Physiol. 14:251–261.

Waring, R.H., B.E. Law, M.L. Goulden, S.L. Bassow, R.W. McCreight, S.C. Wofsy and F.A. Bazzaz. 1995. Scaling gross ecosystem production at Harvard Forest with remote sensing: a comparison of estimates from a constrained quantum-use efficiency model and eddy correlation. Plant Cell Environ. 18:1201–1213.

Wofsy, S.C., M.L. Goulden, J.W. Munger, S.-M. Fan, P.S. Bakwin, B.C. Daube, S.L. Bassow and F.A. Bazzaz. 1993. Net exchange of CO_2 in a mid-latitude forest. Science 260:1314–1317.